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Key innovations, convergence, and success: macroevolutionary lessons from plant phylogeny

Michael J. Donoghue

Abstract.—Improvements in our understanding of green plant phylogeny are casting new light on the connection between character evolution and diversification. The repeated discovery of paraphyly has helped disentangle what once appeared to be phylogenetically coincident character changes, but this has also highlighted the existence of sequences of character change, no one element of which can cleanly be identified as *the* ''key innovation'' responsible for shifting diversification rate. In effect, the cause becomes distributed across a nested series of nodes in the tree. Many of the most conspicuous plant ''innovations'' (such as macrophyllous leaves) are underlain by earlier, more subtle shifts in development (such as overtopping growth), which appear to have enabled the exploration of a greater range of morphological designs. Often it appears that these underlying changes have been brought about at the level of cell interactions within meristems, highlighting the need for developmental models and experiments focused at this level. The standard practice of attempting to identify correlations between recurrent character change (such as the tree growth habit) and clade diversity is complicated by the observation that the ''same'' trait may be constructed quite differently in different lineages (e.g., different forms of cambial activity), with some solutions imposing more architectural limitations than others. These thoughts highlight the need for a more nuanced view, which has implications for comparative methods. They also bear on issues central to Stephen Jay Gould's vision of macroevolution, including exaptation and evolutionary recurrence in relation to constraint and the repeatability of evolution.

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Introduction

Much of Stephen Jay Gould's work was concerned, directly or indirectly, with patterns of character evolution, patterns of clade diversification, and the causal link between these two. Although Gould did not take an explicitly phylogenetic approach to these problems, others have in recent years. In any case, our knowledge of the Tree of Life has expanded enormously (Cracraft and Donoghue 2004) and it is worth considering how phylogenetic insights may be influencing our views on macroevolution and especially the link between character evolution and diversification. In this essay I provide the perspective of someone working on plant evolution, together with a few concrete plant examples. Gould was not, of course, especially interested in plants, but his ideas were clearly intended to apply to organisms of all sorts.

Specifically, I begin by briefly characterizing what we have learned recently about the fundamental structure of green plant phylogeny, drawing a few generalizations about the nature of that progress. Then I consider how this progress has been, or at least should be, affecting our understanding of the connection between character evolution and diversification. My basic argument is that recent phylogenetic findings are making it increasingly difficult to sustain the traditional view of key innovations and also to maintain standard comparative approaches to detecting the effects of character change on diversity. These realizations suggest several new methodological needs and research strategies. In closing I briefly consider how these ideas relate to some of Gould's views on macroevolution.

Progress in Understanding Plant Phylogeny

Figure 1 provides an overview of our present knowledge of phylogenetic relationships among the major lineages of green plants. This is simplified, of course, and consciously rendered pectinate to serve my purposes (see O'Hara 1992, on the representation of trees). Readers are referred to other recent reviews (Bateman et al. 1998; Chapman et al. 1998;

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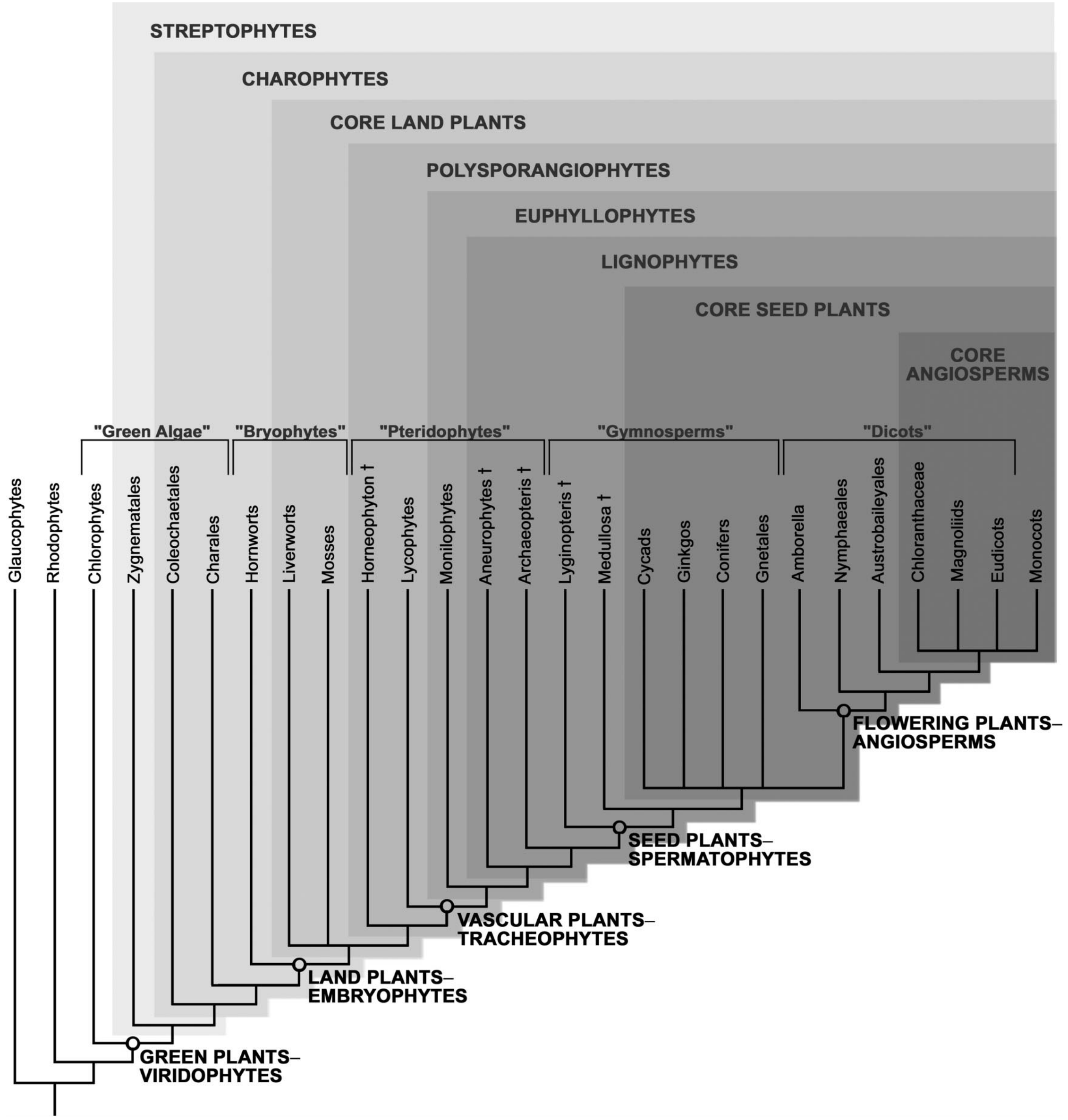


FIGURE 1. An overview of green plant phylogeny, illustrating the recent discovery of major clades (shaded groups); the monophyly of some traditionally recognized groups (shown at nodes with open circles) has been upheld, whereas others are now seen to be paraphyletic (names in quotation marks). † marks denote extinct groups. See text for references and discussion.

Doyle 1998; Kenrick 2000; Donoghue 2002, 2004; Judd et al. 2002; Delwiche et al. 2004; Pryer et al. 2004; Soltis et al. 2004) for references to the primary literature underpinning Figure 1, and for levels of support, commentary on remaining controversies, and a wide variety of evolutionary implications not touched upon here.

Several familiar and long-recognized taxa are strongly supported as monophyletic. These include the entire green plant clade (the viridophytes), land plants (embryophytes), vascular plants (tracheophytes), seed plants (spermatophytes), flowering plants (angiosperms), and monocotyledons (monocots). Conveniently, these clades are marked by characters that relate to their names: green plants by chlorophyll b, land plants by a resting embryo stage in the life cycle (hence embryophytes), vascular plants by vascular tissue with specialized cells for the transport of water (tracheids), seed plants by seeds (integumented megasporangia), flowering plants by one or more carpels in the shortened reproductive axes that we call flowers, and monocots by embryos with just a single seed leaf (cotyledon).

Phylogenetic analyses conducted over the last two decades have also shown that several other traditionally recognized major groups are not monophyletic, but instead represent grades of organization. Specifically, traditional ''green algae,'' ''bryophytes,'' ''pteridophytes'' (seedless vascular plants), ''gymnosperms'' (naked-seed plants), and ''dicotyledons'' appear to be paraphyletic. These had each been diagnosed on the basis of what we now recognize to be ancestral traits. For example, green algae are green plants that lack the specialized characteristics of the land plant clade (they live in the water, lack a resting embryo, etc.). In bryophytes the sporophyte phase is unbranched and lacks vascular tissues of the sort found in tracheophytes. As the names implies, ''seedless vascular plants'' are vascular plants that lack seeds, ''gymnosperms'' are seed plants that lack carpels, and so forth.

Recognition that these traditional groups are paraphyletic has, of course, resulted from the discovery of new major clades that unite one or more of the lineages traditionally assigned to the grade group directly with an included clade. For instance, the dismantling of the traditional green algae came about through the recognition that some groups formerly treated as green algae are actually more closely related to land plants than they are to other green algal lineages. Specifically, it was discovered (initially on the basis of ultrastructural features, but now with much molecular support; [e.g., Karol et al. 2001]) that the Charales and several other lineages (e.g., Klebsormidiales, Zygnematales, Coleochaetales) are more closely related to lands plants than they are to Chlorophyceae, Trebuxiophyceae, and Ulvophyceae (the latter three making up the Chlorophyte clade in the strict sense). The name ''streptophytes'' has now been widely applied to this newly discovered clade (Delwiche et al. [2004], prefer the name ''charophytes;'' see Donoghue 2004).

Similarly, in the first phylogenetic analyses of land plants, hornworts and mosses were found to be more closely related to vascular plants than to liverworts, the other major lineage of ''bryophytes'' (Mishler and Churchill 1985). The term ''stomatophytes'' was coined for this clade, reflecting the presence of stomates in hornworts, mosses, and vascular plants. In recent years, however, several alternative hypotheses have surfaced, especially the idea that the first split was between hornworts and a clade containing the other three clades (e.g., Nickrent et al. 2000; Renzaglia et al. 2000). In any case, phylogenetic analyses that have sampled a sufficient number of representatives of these groups have supported the view that bryophytes do not form a clade but rather represent a grade of organization within land plants.

The name euphyllophytes has recently been applied to the clade including horsetails, whisk-ferns (psilophytes), various fern lineages, and seed plants (e.g., Kenrick and Crane 1997). These are more closely related to one another than to the other extant lineage of seedless vascular plants, the lycophytes. The name ''anthophytes'' was applied to the hypothesized clade including the ''gymnosperm'' group Gnetales along with the flowering plants, to the exclusion of cycads, ginkgos, and conifers (Doyle and Donoghue 1986). As in the bryophyte case, many recent analyses (reviewed by Donoghue and Doyle 2000) do not support this anthophyte clade (Gnetales instead being allied with conifers). In any case, however, ''gymnosperms'' remain paraphyletic relative to angiosperms when fossil groups (e.g., Paleozoic and Mesozoic ''seed ferns'') are considered (Donoghue and Doyle 2000; Pryer et al. 2004); that is, the first seed plants clearly lacked carpels. Finally, within flowering plants, the recently discovered eudicot clade (containing more than 160,000 species) and a re-circumscribed magnoliid clade (containing magnolias, black peppers, avocados, etc.) are found to be more closely related to monocots than they are to some other lineages of ''dicotyledons,'' such

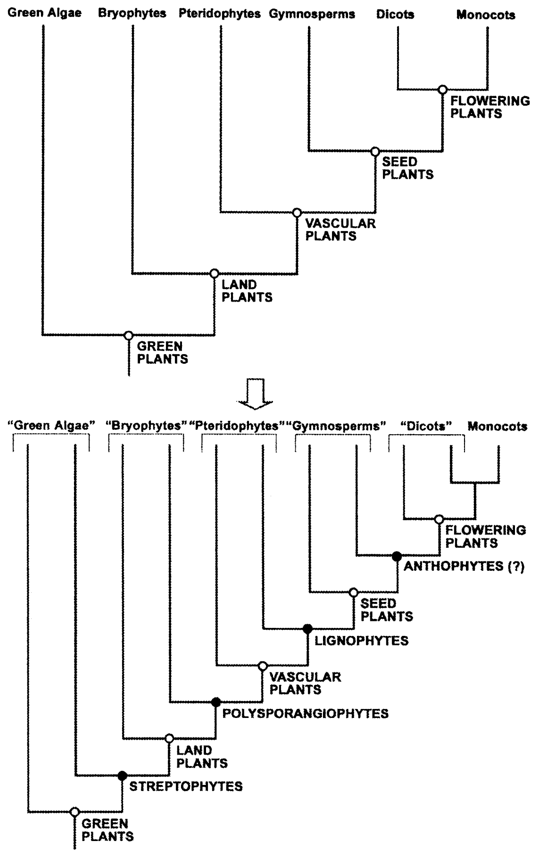


FIGURE 2. The nature of progress in resolving plant phylogeny. The upper tree shows the standard view as of the 1970s; the lower tree depicts current understanding. Major clades supported as monophyletic are marked by open circles at the nodes; newly discovered clades are marked by black circles.

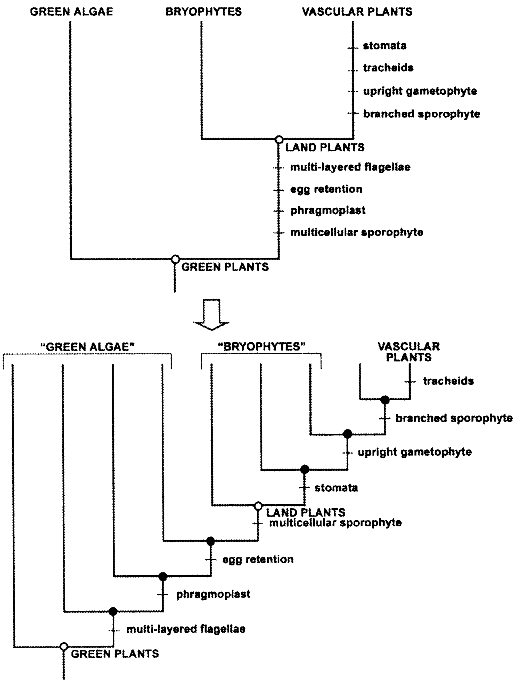


FIGURE 3. An example of the impact of new phylogenetic knowledge (discovery of the paraphyly of "green algae" and "bryophytes") on our understanding of character evolution. What once appeared to be clumped changes at key nodes (upper tree) can now be sorted into a sequence of character changes (lower tree) that clarify the transition to land and the origin of vascular plants.

as *Amborella* and the water-lilies (Zanis et al. 2002; Soltis et al. 2004).

Figure 2 presents a cartoon summary of these results to highlight the nature of the progress that has been made since the 1980s. In general, our advances have entailed confirmation of the monophyly of some long-recognized major clades, along with the recognition of a number of paraphyletic taxa through the discovery of new major clades. Names such as "green algae," "bryophytes," and "dicots" are now either being dropped altogether or being used only to refer to particular life styles or grades of organization. Meanwhile, names such as euphyllophytes and eudicots are finding their way into introductory textbooks (e.g., Judd et al. 2002) and are beginning to orient the way we think about plant diversity and conduct research. The discovery and abandonment of paraphyletic groups is, in general, what progress is all about in phylogenetic systematics (Donoghue 2004).

Character Sequences and Developmental Enablers

How have these advances changed our understanding of plant evolution? The most obvious impact has been on our ability to dissect the evolutionary sequence of events surrounding the greatest transformations in green plant history. For example, consider the transition from life in the water to life on land (see Graham 1993). When green algae and bryophytes were both viewed as clades, this transition appeared to entail a very large number of steps that could not be placed in any particular temporal order (Fig. 3, top). This implied either a large number of extinctions of intermediary taxa and, consequently, major gaps in our knowledge, or a wholesale correlated transformation from one life form to another. Under these circumstances several alternative theories remained viable to explain the evolution of features such as the land plant life cycle, entailing the alternation of multicellular haploid (gametophyte) and diploid (sporophyte) phases. Was a multicellular haploid phase or a multicellular diploid phase added to an ancestral non-alternating life cycle? Or, perhaps the ancestor of land plants belonged to a lineage within which alternation of generations had already evolved. Did the precursors of land plants live in salt water, fresh water, or even on land (several ‘‘green algal’’ lineages independently made the transition to land)? What was the basic body plan from which land plants evolved? After all, ‘‘green algae’’ present an impressive number of alternatives, from unicells, to colonies, to filaments, to pseudo-parenchymatous forms, with or without cell walls separating the nuclei. With no way to sort out the sequence of events, the transition to land largely remained a mystery.

Knowing now that both the traditional green algae and bryophytes are paraphyletic, and having succeeded in identifying the closest living relatives of land plants (Charales and Coleochaetales [Karol et al. 2001]), we can start to establish the sequence of events from the origin of the first green plants through their movement onto land (Fig. 3, bottom). On this basis, we can be quite certain that land plants arose within a lineage of ‘‘green algae’’ living in fresh water, probably quite near the shore. Their ancestors probably had rather complex parenchymatous construction, with gametes (and then zygotes) borne on the parent plant in specialized containers. Perhaps most importantly, we can infer that the land plant life cycle originated through the intercalation of a multicellular diploid phase (by delaying the onset of meiosis) into a life cycle resembling that retained in Coleochaetales and Charales (wherein the diploid zygote undergoes meiosis directly to form haploid spores). Likewise, we can infer that the first land plants had a bryophyte-like life cycle in which the gametophyte was the dominant phase and the sporophyte was smaller and parasitic on the gametophyte.

Moving within land plants, the discovery of the polysporangiophyte clade (Kenrick and Crane 1997; see Pryer et al. 2004) implies that enlargement and branching of the sporophyte preceded the acquisition of tracheids (Fig. 3). Moreover, fossil reconstructions of the gametophytes of the first polysporangiophytes (Remy et al. 1993) suggest that the transition to sporophyte dominance moved through a stage in which gametophyte and sporophyte phases were more or less similar in structure (so-called isomorphic alternation of generations [Kenrick and Crane 1997]).

I provide this level of detail to draw attention to the great significance of recent phylogenetic advances, which have basically settled many major questions about plant evolution. But the main point I want to make here is that recent phylogenetic discoveries don’t just help us to choose among existing hypotheses, but also shed genuinely new light on such problems. Many of the newly discovered green plant clades serve to focus our attention on seemingly minor—but in retrospect apparently quite profound—shifts in the nature of plant development. Prime examples concern meristem structure and function in relation to branching. The polysporangiophyte clade is marked by the ability of the sporophyte plant to branch dichotomously, as compared to the ancestral unbranched condition retained today in the bryophytic lineages (Fig. 4). Dichotomous branching made it possible for a given sporophyte to produce more sporangia and more spores per fertilization event, and perhaps generally to become larger (Mishler and Churchill 1985; Knoll et al. 1986). This ability of the apical meristem to branch apparently set the stage for a series of changes that now mark the tracheophyte clade, notably the evolution of differentiated vascular tissues for the flow of water and nutrients through a larger upright plant body. In retrospect, dichotomous branching may have established the conditions for—or enabled—the evolution of increased size, of vascular tissue, and of many other downstream character changes.

The same line of reasoning applies to the evolution in euphyllophytes of the differentiation between a main axis, or trunk portion of stem, and lateral branches (Fig. 4)—so-called

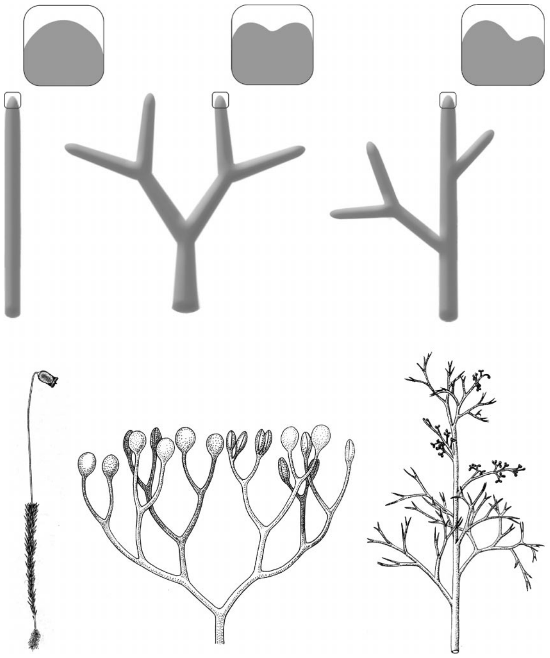


FIGURE 4. A comparison of sporophyte branching among early-branching lineages of land plants. In the bryophytic lineages (left) the sporophyte is unbranched; dichotomous branching evolved at the base of the polysporangiophytes (center); overtopping (or pseudomonopodial growth) evolved at the base of the euphyllophytes (right). Insets at the top represent these differences in branching at the level of the apical meristem. (Drawings at the bottom are from Stewart and Rothwell 1993.)

overtopping or pseudomonopodial growth (Zimmermann 1965). This seemingly minor shift at the level of the shoot apical meristem appears to have enabled the evolution (most likely independently in several lineages [e.g., Boyce and Knoll 2002; but see Schneider et al. 2002; Pryer et al. 2004]) of the determinate lateral organs that we call leaves (or, more specifically, megaphyllous leaves, as distinct from the so-called microphyllous leaves of lycophytes), and, in turn, the evolution of seeds and flowers. These derived traits (e.g., leaves, seeds) are often viewed as the key innovations responsible for the evolutionary success (usually measured in terms of the number of species) of their respective lineages. Recent phylogenetic discoveries have the effect of highlighting subtle, but crucial, underlying developmental shifts at the level of the apical meristem that made possible the evolution of the more obvious characters.

These observations have an important bearing on the identification of ''key innovations.'' In two obvious ways the identification of key innovations becomes easier. First, as already noted, recent progress has distributed inferred character changes across a series of branches as opposed to having them piled up at particular nodes (Fig. 3). The problem with having character changes concentrated at a node is that it is unclear which one (or which combination) of the changes might have triggered a shift in diversification rate. Decomposing such a set of characters can help single out the character(s) associated most directly with shifts in diversification. Second, decomposing paraphyletic groups reduces the number of species in the sister group of the focal clade, thereby increasing the magnitude of the diversity contrast. For example, Charales and Coleochaetales contain many fewer species than did the traditionally circumscribed ''green algae'' (with probably more than 35,000 species). The discovery that Charales (with approximately 500 species) are sister to land plants (with over 300,000 species), and in turn that the Coleochaetales (with about 30 species) are sister to the clade containing these two, greatly accentuates the contrast in diversity between land plants and the several lineages to which they are most closely related. In general, this sort of change makes it easier to locate a significant shift in diversification rate (Moore et al. 2004) and therefore increases the inclination to explain it with reference to a key character change.

However, a third impact of phylogenetic discoveries challenges the very notion of key innovations. The existence in our classifications of major groups such as tracheophytes, spermatophytes, and angiosperms has drawn our attention to the obvious traits of these clades—vascular tissue, seeds, and flowers—as potential drivers of diversification. The discovery of a set of new major clades, including polysporangiophytes, euphyllophytes, lignophytes, etc., likewise focuses our attention on their somewhat more subtle features—dichotomous branching, pseudomonopodial growth, bifacial cambium, etc. The intercalation of these new clades between the traditional groups, I predict, will bring about a subtle but fundamental shift in how we view the link between character evolution and success. Despite the increased ease (just noted) with which we may be able to associate particular character changes with shifts in diversification, I suspect that we will become increasingly less comfortable about phylogenetically localizing ''key'' innovations. Instead, because there are often causal links between characters that evolved earlier and later in a sequence, it will seem increasingly natural to think from the outset about a series of changes culminating in a combination of traits that together served to increase diversification. Appreciating the interdependencies and the combined effects of character changes doesn't just relocate the cause to another node in the tree, but instead distributes the causation across a series of nodes. As we become increasingly aware of the ways in which apparently minor developmental changes early in a chain rendered new morphological designs accessible, we might even be tempted to view early steps as actually necessitating later ones. But the causal links will generally be much more subtle. Overtopping growth did not, we presume, necessitate the evolution of macrophyllous leaves. Instead, it enabled the exploration of a new set of morphological designs, which eventually set the stage for the evolution of leaves.

This refinement in outlook will, I suspect, reveal some important new evolutionary generalities. For example, in the several cases we have been considering (dichotomous branching, overtopping) the enabling changes appear to have been developmental shifts at the level of apical meristems, which presumably involved shifts in gene expression and the localization of signals at the level of cells and cell layers within the meristem. These underlying changes appear now to be highly conserved, in the sense of showing little homoplasy, which perhaps implies that the derived state was somewhat difficult to achieve in the first place and/or that the derived condition rather quickly became burdened by the evolution of dependent traits. Paradoxically, despite the current entrenchment of such traits, they may initially have conferred greater flexibility, opening up new design possibilities and consequently the exploitation (or ''creation'') of new environments.

So far, the basic apical meristem features highlighted here (Fig. 4) have attracted rather little attention from molecular developmental biologists. These characters are, after all, deeply embedded within the phylogeny of green plants, a very great distance from the popular model organisms, and relevant mutations have rarely been recorded. At this stage, even the formulation of credible developmental models, and perhaps the identification of candidate genes and appropriate study organisms, would be quite useful. Along these lines, Geeta (2003) has recently sketched such a model for the origin of dichotomous branching. This entails a duplication in the location of the normal activity of the shoot apical meristem (regulated in part by the KNOX gene pathway), possibly brought about by the periodic expression of so-called MYB genes in the center of the meristem (specifically the ARP genes AS1/rs2/phan). My hope is that speculation of this type will encourage more careful comparisons and experimental work in the relevant organisms (e.g., the apex of the moss sporophyte, branching in lycophytes).

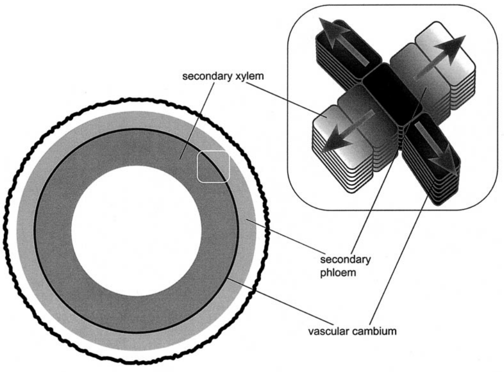
Convergence and Equivalence

New phylogenetic results will also, I believe, bring about a shift in how we interpret the significance of the recurrence of similar character states in different lineages. We have rightly viewed such cases as providing opportunities to test the effect of the evolution of a trait of interest on the evolution of other traits or on diversification rate. A repeated association between the evolution of a trait and elevated diversification rates suggests a causal connection. This seems reasonable, so long as we also appreciate that the effect might be somewhat indirect, or a function of the accumulation of characters, as discussed above. However, rather little attention has been paid to negative results—for example, where a trait is associated with increased diversification in one or a few lineages, but not in other lineages, and the correlation ends up looking weak with respect to a predicted consistent effect. One has the sense that such mixed results are the norm, although this is difficult to assess because such ''insignificant'' results tend not to be published.

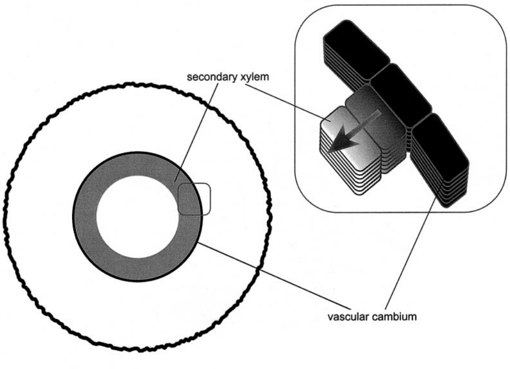
What are we to make of such cases? One interpretation has recently been discussed by de Queiroz (2002), namely that the influence of a particular sort of character change is contingent on other factors. That is, for example, the origin of a particular state in a particular environment (say, the herbaceous habit in a terrestrial setting) may have a positive effect on diversification, whereas the evolution of the ''same'' trait in a different environment (say, herbaceousness in an aquatic habitat) might have little influence on diversification, or maybe even a negative effect. Feild et al. (2004) emphasized the critical role of the environmental context in understanding the function and the effect on diversification of such ''key'' angiosperm characters as vessels and closed carpels.

This is an excellent point, but another interpretation also comes to mind. Maybe some ways of making a trait are really somehow ''better'' than others. After all, traits that evolved independently in separate, distantly related lineages are apt to be truly convergent (as opposed to parallel) in the sense of having been constructed from different starting points, and possibly in quite different ways. Those differences might ultimately be of great significance in terms of both the subsequent evolutionary changes that they enable and lineage ''success.'' Some ways of ''solving'' a problem might ultimately be better than others in the sense of allowing greater evolutionary flexibility.

Several cases from plant evolution come to mind, especially related to changes in organism size and longevity. The tree growth habit (tall plants, with a thickened single trunk, branching well above ground level) evolved many times independently—in lycophytes, equisetophytes, and lignophytes (Fig. 1), to name a few prominent cases (others cases are discussed briefly below). These cases all involved the same basic mechanism, namely the production in the stem of a cylinder of cambium—a secondary meristematic tissue that produces new cells to the inside and/or the outside of the stem, thereby increasing the girth of the stem. This, in concert with the evolution of a variety of mechanical support systems, allowed the evolution of large trees (Niklas 1997). Importantly, however, painstaking paleobotanical studies have shown that the cambium functioned differently in these different clades. In lignophytes (including the ''progymnosperms,'' such as *Archaeopteris*, and seed plants) we find the familiar situation, in which the cambium is ''bifacial''—producing secondary xylem tissue toward the center of the stem and secondary phloem tissue toward the outside (Fig. 5, top). By contrast, extinct tree lycophytes and equiseto-



Bifacial cambium



Unifacial cambium

FIGURE 5. Differences between the bifacial cambium in the lignophyte lineage (including seed plants) and the unifacial cambium found in extinct tree lycophytes (e.g., *Lepidodendron*). The bifacial cambium produces both secondary xylem and secondary phloem, and the cambial initials are able to divide both periclinally (producing cells that differentiate in secondary tissues) and anticlinally (producing new cambial initials). The unifacial cambium produced only secondary xylem and the cambial initials divided only periclinally, limiting expansion of the cambial cylinder and the production of wood. These seemingly minor differences translated into major differences in evolutionary flexibility and ''success'' (see text).

phytes are reconstructed as having had a unifacial cambium (Eggert 1961, 1962; Cichan and Taylor 1990). They produced cells only to the inside, which differentiated as secondary xylem tissue, but not toward the outside to be differentiated as secondary phloem (Fig. 5, bottom). Secondary phloem appears to have been entirely lacking in these plants (Eggert 1972; Eggert and Kanemoto 1977).

Both types of construction allowed the evolution of large trees, but the differences in detail appear to have had profound consequences. The familiar seed plant cambium originated in the Devonian at the base of the lignophyte clade. Rather shortly thereafter, by the end of the Devonian, the major lineages of seed plants (aside from the angiosperms) had come into existence, including a variety of ''seed fern'' groups (looking rather like modern tree ferns), cycad-like plants, conifer-like plants, etc. This radiation spawned highly successful lineages of woody plants from the standpoint of their longevity, structural diversity, and species numbers.

By contrast, today there are only perhaps 1200 species of lycophytes, the vast majority of which (e.g., *Selaginella*, with approximately 700 species) represent lineages that retained the ancestral herbaceous habit and never included trees. Large lycophyte trees evolved (perhaps several times) within a clade characterized by heterospory (i.e., the production of two kinds of spores) and a flaplike ''ligule'' associated with each leaf, and they diversified and became widespread especially during the Carboniferous. *Isoetes* (so-called quillworts), containing perhaps 150 species of small rosette plants, is the only living descendant of the lycophyte line in which secondary growth evolved—these plants have retained a cambium and ''rootlets'' that resemble those of the extinct trees (Gifford and Foster 1989). However, *Isoetes* probably originated within the so-called cormos line of lycophytes (including *Chaloneria* and *Pleuromeia*), which never attained the great size of *Lepidodendron* and the other very large lycophyte trees. There are no living representatives of this ''rhizomorphic'' lineage. Similarly, the equisetophyte lineage (horsetails and relatives), which was diverse and produced large trees in the Carboniferous, is represented today by just 15 species of *Equisetum* (Des Marais et al. 2003), all of them relatively small plants lacking wood.

Although the down-sizing of the lycophyte and equisetophyte clades (in both plant stature and species number) may not be directly or entirely attributable to the structure of their wood, the unifacial cambium does seem to have placed significant functional constraints on the evolution of these plants—constraints that are reflected in a variety of other characteristics. First, relative to lignophytes with the bifacial cambium, the unifacial plants produced rather little wood. This was not a function of the unifacial cambium per se, but rather of the apparent inability of these plants to expand greatly the circumference of the cambial cylinder (Cichan and Taylor 1990). Cambial cells in lignophytes can undergo both periclinal and anticlinal cell divisions, the periclinal ones adding xylem and phloem and the anticlinal ones adding extra cells to the ring of cambium (Fig. 5). By contrast, cambial cells in unifacial plants apparently did not divide anticlinally. Consequently, any increases in the cambial ring were brought about by the growth of cambial initials in length, spreading apart the cambial initials situated just above and below them in the cambial cylinder. This mechanism can produce only very limited circumferential increases, and the girth of these plants may have resulted largely from something analogous to the primary thickening meristem found today in palm trees (see below; Bateman et al. 1992; Bateman 1994). The paucity of wood formed by these plants apparently had several other consequences. For one thing it meant that the wood that was produced had to be especially efficient, and achieving this entailed structural changes in the vascular tissue and the tracheary elements themselves (Cichan 1986). Also, because the wood of these plants could provide only minimal mechanical support (as compared with lignophyte trees), in the lycophyte line a peculiar barklike ''periderm'' tissue (situated in the outer cortex, beneath the persistent leaf bases) was ''invented'' to stiffen the trunk.

Other peculiar attributes of these plants reflect the lack of secondary phloem. In lignophytes, secondary phloem makes possible the

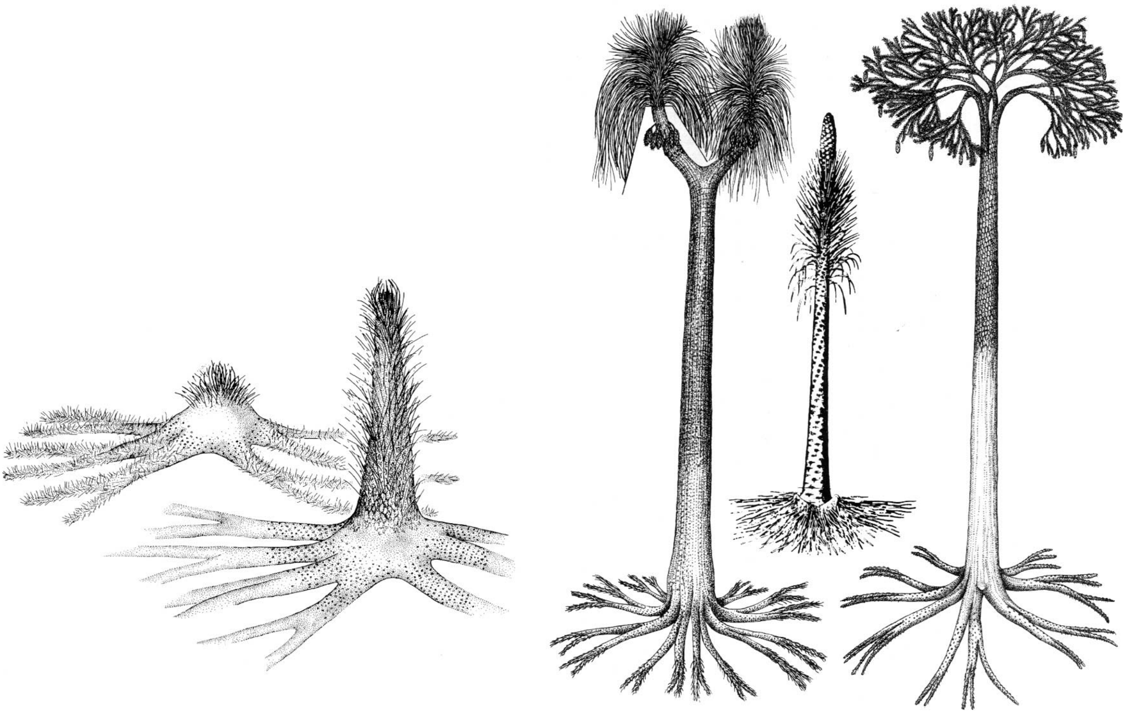


FIGURE 6. A sample of growth forms in extinct lycophytes. Two drawings on the left (from Phillips and DiMichele 1992) show early stages in the life cycle—establishment of the stigmarian ''root'' system with possibly photosynthetic ''rootlets'' prior to rapid stem elongation. Three drawings on the right (from Stewart and Rothwell 1993) show reconstructed forms of the determinate stems (not drawn to the same scale); from left to right: *Sigillaria*, *Pleuromeia*, and *Lepidodendron*.

transport of carbohydrates from sites of photosynthesis (typically leaves) to distant parts of the plant, such as the roots. In the absence of secondary phloem, such long-distance transport would be severely limited, which would necessitate the maintenance of photosynthesizing structures in the vicinity of tissues that needed to stay alive in order to function. Consequently, in the unifacial lineages we find several highly unusual strategies. Focusing now on lycophyte trees, we see the maintenance of photosynthesizing leaf bases all over the stems (and, consequently, the absence of normal bark as in seed plant trees). These plants probably also provisioned their massive so-called stigmarian ''root'' systems by producing photosynthesizing ''rootlets'' (probably leaf homologs), some of which appear to have been deployed above ground or into shallow water in the swamps that most of these plants occupied (Fig. 6) (Phillips and DiMichele 1992).

The truly weird life cycles inferred for these plants (Andrews and Murdy 1958; Eggert 1961; DiMichele and Phillips 1985; Phillips and DiMichele 1992) are also probably related to the lack of secondary phloem. It appears that the large lycophyte trees grew very little in height for many years, instead remaining stumplike while the stigmarian system became well established underground (Fig. 6). Then they bolted up to great heights, quickly produced their spores (repeatedly, or only once), and then died. In effect, the enormous above-ground stems behaved like the inflorescences of other plants. This highly unusual determinate growth mode (also found in equisetophyte trees) may have been, in part, a means of avoiding the long-term maintenance of dispersed functioning tissues without secondary phloem and the production of costly mechanical support tissues.

As noted above, the tree habit evolved in other lineages as well (Fig. 7). For example, arborescent forms are found among extinct marattialean (*Psaronius*) and filicalean (*Tempskya*)

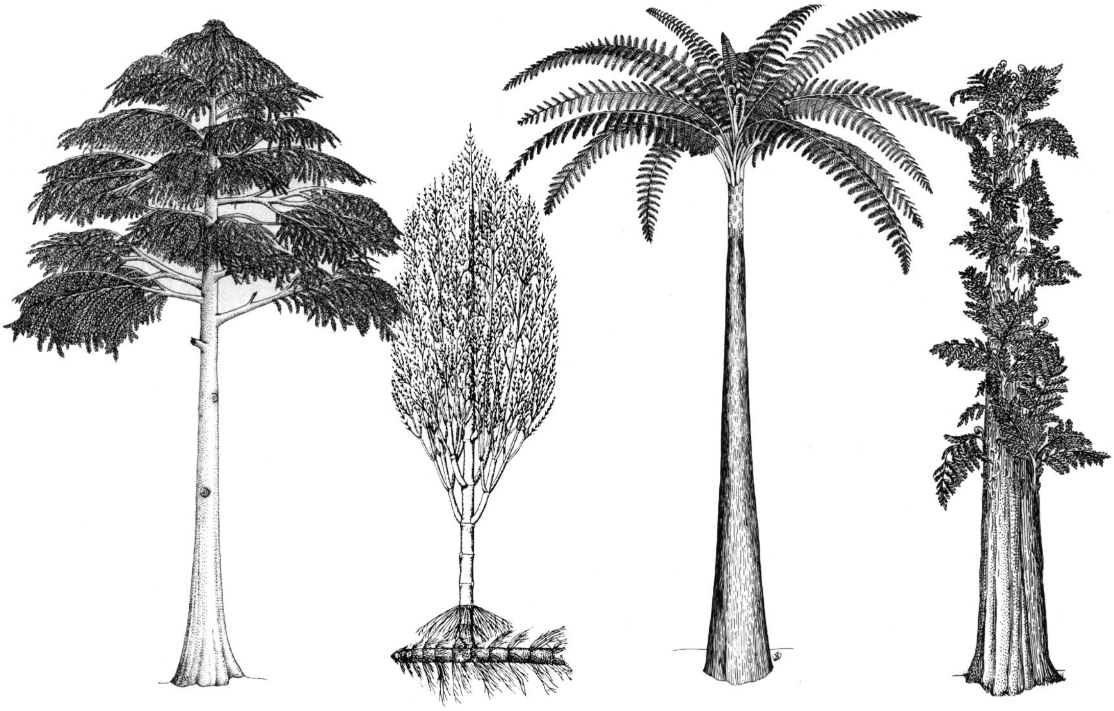


FIGURE 7. Diversity of form among extinct treelike plants from the Devonian and Carboniferous (not drawn to the same scale). From left to right: *Archaeopteris* (an early lignophyte); *Calamites* (an equisetophyte); *Psaronius* (a marattialean ''fern''), in which the trunk was formed by a mantle of adventitious roots; *Tempskya* (a filicalean ''fern''), in which the trunk was formed by numerous smaller stems embedded in a tangle of adventitious roots.

ferns, and in modern tree ferns (Cyatheaceae). Trees were also re-evolved several times within the ancestrally herbaceous monocotyledonous flowering plants, with palm trees providing a prime example. In each of these cases the tree habit was achieved in a distinctly different way, and again in each case with obvious downstream consequences (Niklas 1997). In the upper Paleozoic *Psaronius* (Fig. 7) and in extant tree ferns, a cambium is lacking, and increased girth and mechanical support are provided by a mantle of adventitious intertwining roots. Cross-sections of the trunk of *Tempskya* reveal yet another way to make a tree—its ''false'' stems were made of many smaller ramifying stems (each lacking secondary growth) packed in among a dense thicket of adventitious roots (Andrews 1948). Similar construction is found today in the osmundaceous fern *Todea*. Palms also lack a vascular cambium, and increases in diameter are largely due to what is called a primary thickening meristem, situated in a zone where the young leaves attach to the stem (Rudall 1991; Tomlinson 1995). Their mechanical strength is provided by a combination of a greater density of vascular bundles in the outer cortical tissue and thickening of the cell walls in that region (Niklas 1997). Some other monocots, within a variety of separate lineages living mostly in arid regions (e.g., Agavaceae, Convalariaceae, Iridaceae, Xanthorrhoeaceae [Chase et al. 2000]), have also become trees (Tomlinson and Zimmermann 1969; Tomlinson 1995). As in the palms, the presence of vascular bundles that appear ''scattered'' in the stem (an atactostele) and of individual bundles that are ''closed'' to further growth (both conditions associated with the origin of the monocots) effectively precluded the re-evolution of a ''normal'' ring of cambium. Instead, these plants invented a novel form of unifacial cambium (the ''etagen'' cambium), situated near the periphery of the stem, which yields derivatives that differentiate as additional ground tissue and into whole new vascular bundles containing both xylem and phloem (Rudall 1991; Tomlinson 1995).

The point of giving these details about tree construction is to illustrate that different ways of attaining a given condition, evolved convergently in different lineages, can be constrained by prior circumstances (e.g., the reinvention of a cambium in monocots with scattered bundles) and, most importantly for present purposes, can sometimes have significant consequences for subsequent evolution in those lineages (e.g., the bizarre structures and life cycles of lycophytes). Such differences among lineages might translate into ''negative'' or only weakly positive results in standard phylogenetic comparative tests for character correlations or for correlations with diversity. As explained in the next section, I do not intend this as an argument against attempting to identify common evolutionary responses to convergent characters across lineages. Instead, I hope to highlight the potential power of negative results in such tests in helping to pinpoint consequential differences in ''the same'' structure, thereby refining the initial causal hypothesis.

Some Methodological Implications

Phylogenetic discoveries have been affecting macroevolutionary studies in a variety of completely obvious ways. In general, in trying to make sense of the tempo and mode of macroevolution it helps to know how species are related to one another. The point of my paper is that some much less obvious, but ultimately more fundamental, effects are on the horizon. Presently, we tend to want to pin the cause of the ''success'' of a clade on a ''key innovation''—used here to refer to a trait responsible for increasing the rate of diversification (see Givnish 1997; Sanderson 1998; and Hunter 1998; for alternative views on ''key innovation'' and ''adaptive radiation''). Tests of evolutionary character relationships and key innovation hypotheses hinge on phylogenetic correlations. Does the character of interest really correlate with a shift in diversification? Do we see repeated instances, in different clades, of such a correlation?

I made the case above that key innovations may not happen at a point in a tree, but over a region. Likewise, shifts in diversification may ratchet upward (or downward) not at a single spot in a tree, but over a series of nodes. New comparative methods need to be designed with this image in mind. We need tests that attempt to identify particular sequences of change that may have impacted diversification, as well as clusters of positive, but perhaps individually less than significant, shifts in diversification rate (see Moore et al. 2004 for some methodological developments along these lines).

Likewise, in testing for repeated evolutionary correlations, more attention needs to be paid to potentially significant character differences in different clades. In the case of truly convergent characters, as illustrated by the evolution of the tree habit, differences in constructional details can have profound effects on subsequent evolution and, ultimately, on what we judge to be clade success. Failure to identify a significant correlation in a phylogenetic test could reflect such underlying differences and might help to refine the comparison. Ultimately, of course, it is critical to specify a particular mechanistic connection between the evolution of a trait and the evolution of other traits and/or diversification rate. Formulating the causal hypothesis as precisely as possible will more clearly circumscribe which instances of ''the same'' character are relevant in performing a test (see Coddington 1994).

In many cases I imagine that an initial phylogenetic test will narrow the set of comparisons to characters with more specific similarities, perhaps often to cases of the parallel evolution of states in the strict sense (involving the same structural modifications and presumably the same genes, and therefore perhaps in more closely related organisms; see discussion in the next section). But, this is not to say that phylogenetic correlation tests are properly applied only to parallel changes. Instead, because the outcome, whether one uses wildly convergent or only strictly parallel changes, is potentially of interest, I am suggesting a nested data exploration strategy, beginning perhaps with obviously convergent traits and narrowing down the comparison depending on the results. For example, it seems well worth testing whether the tree habit, regardless of how it was actually attained, had a significant effect on the evolution of other traits or on patterns of diversification. Likewise, to mention another popular case in the plant literature (e.g., Donoghue 1989; Heilbuth 2000; Vamosi et al. 2003), it is worthwhile testing whether dioecy and fleshy, bird-dispersed propagules are correlated, or whether either one has influenced diversification, regardless of major structural differences (e.g., whether the actual fleshy structure is the wall of the seed, the wall of the fruit, or some accessory structure). But, where very different structures are involved, we should not be surprised or disappointed by negative or ambiguous results. Instead, we should learn from such experiences that structural details might make a difference with respect to the presumed mechanistic hypothesis, and then design more refined comparisons. Such refinements should take account of different organismal and environmental contexts (de Queiroz 2002), but they also should take more seriously the distinction between convergence and parallelism, which is often glossed over in such work.

Some Connections to Gould

These observations connect to Steve Gould's thoughts in a variety of ways. Gould presumably would have appreciated the idea of developmental enablers—changes early in a sequence that opened up new design options. But, exactly how such traits relate to Gould's concepts and terminology is a bit complicated. In my examples the underlying changes that set the stage for later, more obvious changes are themselves, I presume, adaptations. They are what once would have been labeled ''preadaptations,'' a term that Gould rejected on the grounds of its being '' 'prepackaged' for inevitable trouble and misunderstanding'' (Gould 2002: p. 1232). Gould and Vrba (1982) introduced the term ''exaptation'' to cover any instance of co-optation, whether from a previous adaptation or from a nonaptation, but they emphasized that ''exaptations that began as nonaptations represent the missing concept'' (Gould and Vrba 1982: p. 12). Unfortunately, they left this more specific concept unnamed. Gould (2002: p. 1278), therefore, recently distinguished between what he called ''franklins'' (''alternative potential functions of objects now being used in another way'') and ''miltons'' (''currently unused material organs and attributes'') as the basic elements of the ''exaptive pool.'' As he pointed out, ''franklin'' captures the concept behind the term preadaptation and ''milton'' captures the notion of nonaptations available for co-opting. Where do my plant examples fall in this expanded terminology? If I'm forced to use Gould's terms (which I must admit I have a hard time taking seriously), then my examples are very likely ''franklins.'' That is, the underlying traits that I have described as developmental enablers (e.g., dichotomous branching, overtopping) were probably adaptations in their own right, but they also clearly provided inherent potential for future exaptive changes (e.g., to pseudomonopodial growth, leaves).

Having claimed that these cases are franklins, I hasten to note that I think there are also important miltons in plants, which have also been brought to light in phylogenetic analyses. For example, in recent studies of the angiosperm clade Dipsacales (a group of around 1100 species of Asteridae), we have discussed the evolution of a specialized structure called an ''epicalyx'' (Donoghue et al. 2003). It appears that the epicalyx evolved (possibly twice, in Dipsacaceae and in Morinaceae) through modification of several sets of subtending ''supernumerary'' bracts, which we interpret as having been ''left over'' from the earlier loss of flowers in the inflorescence (Donoghue et al. 2003). If so, the supernumerary bracts are miltons that were co-opted to form the epicalyx. It is difficult to quantify at this stage, but in view of the nature of plant morphology, and especially the evolutionary use and reuse of ''leaves'' for a very wide variety of purposes, I suspect that the co-optation of miltons has been quite common in plant evolution. As for Gould's distinctions between ''spandrels,'' ''manumissions,'' and ''insinuations'' (Gould 2002: p. 1278), I won't attempt to further categorize the epicalyx. In this case, and in the other real examples that come to mind, these categories do not seem mutually exclusive enough to warrant the formality.

My discussion of convergence and success intersects another area of relevance to Gould's thought, namely the distinction between parallelism and convergence, which he portrayed as critical for properly understanding the notion and the extent of ''historical constraint.'' Parallelisms, he argued, reveal historical constraints in the evolving system—the same condition originates again and again within a lineage owing to something about the structure and development of the shared ancestor. Convergences, on the other hand, demonstrate the power of natural selection to fashion similar forms from very different starting points. Here again there are terminological issues. Gould (2002) provided a fine analysis of the convergence-parallelism distinction but settled on a terminology that I think may not be ideal. As he stressed, E. Ray Lankester, who coined the term ''homoplasy'' in 1870, viewed it (ironically) as a form of homology (equivalent to Owen's ''general homology''). Specifically, Lankester meant to apply it to ''independently evolved, but historically constrained, similarities—what we would now call parallelisms'' (Gould 2002: p. 1073). Nevertheless, Gould chose to follow standard practice in applying ''homoplasy'' very broadly to all sorts of non-homology, including both parallelism and convergence.

My own preference is to use ''analogy'' for all non-homologous similarities (e.g., as Osborn did in 1905), and to use ''homoplasy'' in the more restricted (and original) sense to refer to parallelisms. ''Homoplasy'' would then refer precisely to the sorts of recurrent similarities detected in phylogenetic analyses. That is, it would refer to recurrences in the states of characters that are actually included in phylogenetic analyses on the working assumption that they are truly homologous because they pass Remane's positional, structural, and developmental tests of homology (Patterson 1982; Donoghue 1992). By contrast, convergences fail such tests and are excluded at the outset (as individual characters) from phylogenetic analyses. Applying the terms in this way would serve to connect these abstract discussions directly to work on levels of homoplasy in the phylogenetic literature (e.g., Sanderson and Donoghue 1989, 1996). Metrics of the extent of parallelism (e.g., the consistency index) could then help to quantify the importance of historical constraint.

But, leaving aside these terminological issues, I quite agree with Gould that the parallelism-convergence distinction is important from the standpoint of what it implies about the mechanisms underlying character change. However, the point of my examples is different, namely that the distinction is also important because parallelisms and convergences may have rather different long-term evolutionary consequences. The tree habit as manifested by lycophytes had very different consequences (in terms of the evolution of other characters, and long-term success) than did the tree habit as it evolved in lignophytes. Making (or failing to make) the convergence-parallelism distinction can have important consequences for comparative tests, and I have suggested a strategy of nested tests beginning with clear instances of convergence and working toward parallelisms.

This last statement implies the existence of a continuum between parallelism and convergence, which Gould also clearly appreciated and used to his advantage. His basic argument was that (1) parallelisms are important because they reveal constraints due to deeper homology, and (2) recent developmental studies have revealed that many instances of supposed convergence are actually at least in part cases of parallelism. Therefore, (3) constraint has been even more pervasive than we might have supposed. The critical link in his argument is the contention that many real cases show signs of both convergence and parallelism, a point he illustrated with examples such as the role of the *Pax-6* gene in the evolution of eyes in different animal lineages. So, what begins as a plea for paying more attention to the convergence-parallelism distinction ends up stressing that the distinction is a blurry one at best. My guess is that this blurriness is even more pervasive than Gould imagined. In plants, at least, with their modular, open developmental systems, David Baum and I (Baum and Donoghue 2002) have argued that cases of mixed or partial homology (see Sattler 1984, 1991) may be common owing to ''transference of function,'' especially between adjacent organs, brought about by shifts in the location where genes are expressed (what we termed ''homeoheterotopy''). The epicalyx in Dipsacales, mentioned above, may provide a concrete example. That is, the calyx-like appearance and function of the epicalyx might reflect the activation of calyx identity genes in a newly formed structure adjacent to the calyx (Donoghue et al. 2003). In the end, it may be difficult to sustain the notion of pure convergence, a thought that I suppose Gould would have enjoyed.

Finally, these thoughts about recurrence also bear on the issue of the role of convergence vis-à-vis the repeatability of evolution (Gould 1989; Conway Morris 1998, 2003; Conway Morris and Gould 1998). Convergences, parallelisms, and mixtures of the two surely will occur in any evolving systems, and at least for parallelisms we can make concrete predictions about the frequency of occurrence (depending on the number of branching events, the number of character states, and rates of character evolution [Donoghue and Ree 2000]). But the mere fact of recurrence, I would argue, does little to guarantee convincing repeat performances in running the tape of Life over again. The idea of convergence is that structures are put together in different ways from different starting points in different lineages. If my argument is correct that differences in construction (even seemingly minor ones) can have major effects on downstream evolutionary changes and patterns of diversification, then convergence on the same basic form in different iterations might yield wildly different outcomes. Large size, for example, may be selected again and again, but depending on the details of how large size is actually attained, we might end up with very different sorts of organisms. In one iteration we might get familiar-looking lignophyte-like trees (e.g., imagine a pine tree, or a maple), but in the next iteration we might see giant clubmosses or horsetails, and in a third go-around the world might fill up with palm trees. Although there may be commonalities in what is selected for, different mechanisms underlying the response could translate into enormous differences in structure, life cycles, patterns of ''success,'' ecological communities, and so on. So, approaching the problem from a different angle, I end up squarely on Gould's side of this particular argument.

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Literature Cited

Andrews, H. N. 1948. Fossil tree ferns of Idaho. Archaeology 1: 190–195.

Andrews, H. N., and W. H. Murdy. 1958. *Lepidophloios* and ontogeny in arborescent lycopods. American Journal of Botany 45:552–560.

Bateman, R. M. 1994. Evolutionary-developmental change in the growth architecture of fossil rhizomorphic lycopsids: scenarios constructed on cladistic foundations. Biological Reviews of the Cambridge Philosophical Society 69:527–597.

Bateman, R. M., W. A. DiMichele, and D. A. Willard. 1992. Experimental cladistic analyses of anatomically preserved arborescent lycopsids from the Carboniferous of Euramerica: an essay in paleobotanical phylogenetics. Annals of the Missouri Botanical Garden 79:500–559.

Bateman, R. M., P. R. Crane, W. A. DiMichele, P. R. Kenrick, N. P. Rowe, T. Speck, and W. E. Stein. 1998. Early evolution of land plants: phylogeny, physiology and ecology of the primary terrestrial radiation. Annual Review of Ecology and Systematics 29:263–292.

Baum, D. A., and M. J. Donoghue. 2002. Transference of function, heterotopy, and the evolution of plant development. Pp. 52–69 *in* Q. Cronk, R. Bateman, and J. Hawkins, eds. Developmental genetics and plant evolution. Taylor and Francis, London.

Boyce, C. K., and A. H. Knoll. 2002. Evolution of developmental potential and the multiple independent origins of leaves in Paleozoic vascular plants. Paleobiology 28:70–100.

Chapman, R. L., M. L. Buchheim, C. F. Delwiche, T. Friedl, V. A. R. Huss, K. G. Karol, L. A. Lewis, J. Manhart, R. M. McCourt, J. L. Olsen, and D. A. Waters. 1998. Molecular systematics of green algae. Pp. 508–540 *in* D. Soltis, P. Soltis, and J. Doyle, eds. Systematics of plants II. Kluwer Academic, New York.

Chase, M. W., D. E. Soltis, P. S. Soltis, P. J. Rudall, M. F. Fay, W. J. Hahn, S. Sullivan, J. Joseph, M. Molvray, P. J. Kores, T. J. Givnish, K. J. Sytsma, and J. C. Pires. 2000. Higher-level systematics of the monocotyledons: an assessment of current knowledge and a new classification. Pp. 3–16 *in* K. Wilson and D. Morrison, eds. Monocots: systematics and evolution. CSIRO Publishing, Collingwood, Victoria, Australia.

Cichan, M. A. 1986. Conductance of the wood of selected Carboniferous plants. Paleobiology 12:302–310.

Cichan, M. A., and T. N. Taylor. 1990. Evolution of cambium in geological time—a reappraisal. Pp. 213–228 *in* M. Iqbal, ed. The vascular cambium. Wiley, Somerset, U.K.

Coddington, J. A. 1994. The role of homology and convergence in studies of adaptation. Pp. 53–78 *in* P. Eggleton and R. Vane-Wright, eds. Phylogenetics and ecology. Academic Press, London.

Conway Morris, S. 1998. The crucible of creation. Oxford University Press, Oxford.

———. 2003. Life's solution: inevitable humans in a lonely universe. Cambridge University Press, Cambridge.

Conway Morris, S., and S. J. Gould. 1998. Showdown on the Burgess shale. [The Challenge by Conway Morris and the Reply by S. J. Gould.] Natural History 107:48–55.

Cracraft, J., and M. J. Donoghue, eds. 2004. Assembling the tree of life. Oxford University Press, New York.

Delwiche, C. F., R. A. Anderson, D. Bhattacharya, B. D. Mishler, and R. M. McCourt. 2004. Algal evolution and the early radiation of green plants. Pp. 121–137 *in* Cracraft and Donoghue, 2004.

de Queiroz, A. 2002. Contingent predictability in evolution: key traits and diversification. Systematic Biology 51:917–929.

Des Marais, D. L., A. R. Smith, D. M. Britton, and K. M. Pryer. 2003. Phylogenetic relationships and evolution of extant horsetails, *Equisetum*, based on chloroplast DNA sequence data (*rbc*L and *trn*L-F). International Journal of Plant Sciences 164:737–751.

DiMichele, W. A., and T. L. Phillips. 1985. Arborescent lycopod reproduction and paleoecology in a coal-swamp environment of Late Middle Pennsylvanian age (Herrin Coal, Illinois, USA). Review of Paleobotany and Palynology 44:1–26.

Donoghue, M. J. 1989. Phylogenies and the analysis of evolutionary sequences, with examples from seed plants. Evolution 43:1137–1156.

———. 1992. Homology. Pp. 170–179 *in* E. Keller and E. Lloyd, eds. Keywords in evolutionary biology. Harvard University Press, Cambridge.

———. 2002. Plants. Pp. 911–918 *in* M. Pagel, ed. Encyclopedia of evolution, Vol. 2. Oxford University Press, Oxford.

———. 2004. Immeasurable progress on the Tree of Life. Pp. 548–552 *in* Cracraft and Donoghue, 2004.

Donoghue, M. J., and J. A. Doyle. 2000. Demise of the anthophyte hypothesis? Current Biology 10:R106–R109.

Donoghue, M. J., and R. H. Ree. 2000. Homoplasy and developmental constraint: a model and an example from plants. American Zoologist 40:759–769.

Donoghue, M. J., C. D. Bell, and R. C. Winkworth. 2003. The evolution of reproductive characters in Dipsacales. International Journal of Plant Sciences 164:S453–S464.

Doyle, J. A. 1998. Phylogeny of the vascular plants. Annual Review of Ecology and Systematics 29:567–599.

Doyle, J. A., and M. J. Donoghue. 1986. Seed plant phylogeny and the origin of angiosperms: an experimental cladistic approach. Botanical Review 52:321–431.

Eggert, D. A. 1961. The ontogeny of Carboniferous arborescent Lycopsida. Palaeontographica Abteilung B 108B:43–92.

———. 1962. The ontogeny of Carboniferous arborescent Sphenopsida. Palaeontographica 110B:99–127.

———. 1972. Petrified *Stigmaria* of sigillarian origin from North America. Review of Paleobotany and Palynology 14:85–99.

Eggert, D. A., and N. Y. Kanemoto. 1977. Stem phloem of Middle Pennsylvanian *Lepidodendron*. Botanical Gazette 138:102–111.

Feild, T. S., N. C. Arens, J. A. Doyle, T. E. Dawson, and M. J. Donoghue. 2004. Dark and disturbed: a new image of early angiosperm ecology. Paleobiology 30:82–107.

Geeta, R. 2003. Variation and diversification in plant evo-devo [book review]. American Journal of Botany 90:1257–1261.

Gifford, E. M., and A. S. Foster. 1989. Morphology and evolution of vascular plants, 3d ed. W. H. Freeman, New York.

Givnish, T. J. 1997. Adaptive radiation and molecular systematics: issues and approaches. Pp. 1–54 *in* T. Givnish and K. Sytsma, eds. 1997. Molecular evolution and adaptive radiation. Cambridge University Press, Cambridge.

Gould, S. J. 1989. Wonderful life: the Burgess shale and the nature of history. Norton, New York.

———. 2002. The structure of evolutionary theory. Harvard University Press, Cambridge.

Gould, S. J., and E. S. Vrba. 1982. Exaptation—a missing term in the science of form. Paleobiology 8:4–15.

Graham, L. E. 1993. Origin of the land plants. Wiley, New York.

Heilbuth, J. C. 2000. Lower species richness in dioecious clades. American Naturalist 156:221–241.

Hunter, J. P. 1998. Key innovations and the ecology of macroevolution. Trends in Ecology and Evolution 13:31–36.

Judd, W. S., C. S. Campbell, E. A. Kellogg, P. F. Stevens, and M. J. Donoghue. 2002. Plant systematics: a phylogenetic approach, 2d ed. Sinauer, Sunderland, Mass.

Karol, K. G., R. M. McCourt, M. T. Cimino, and C. F. Delwiche. 2001. The closest living relatives of land plants. Science 294: 2351–2353.

Kenrick, P. 2000. The relationships of vascular plants. Philosophical Transactions of the Royal Society of London B 355: 847–855.

Kenrick, P, and P. R. Crane. 1997. The origin and early diversification of land plants: a cladistic study. Smithsonian Institution Press, Washington, D.C.

Knoll, A. H., S. W. F. Grant, and J. W. Tsao. 1986. The early evolution of land plants. *In* T. Broadhead, ed. Land plants: notes for a short course. Studies in Geology 15:45–63. Department of Geology,University of Tennessee, Knoxville.

Lankester, E. R. 1870. On the use of the term homology in modern zoology, and the distinction between homogenetic and homoplastic agreements. Annals of the Magazine of Natural History, 4th series, 6:34–43.

Mishler, B. D., and S. P. Churchill. 1985. Transition to a land flora: phylogenetic relationships of the green algae and bryophytes. Cladistics 1:305–328.

Moore, B. R., K. M. A. Chan, and M. J. Donoghue. 2004. Detecting diversification rate variation in supertrees. Pp. 487–533 *in* O. Bininda-Emonds, ed. Phylogenetic supertrees: combining information to reveal the tree of life. Kluwer Academic, New York.

Nickrent, D., C. L. Parkinson, J. D. Palmer, and R. J. Duff. 2000. Multigene phylogeny of land plants with special reference to bryophytes and the earliest land plants. Molecular Biology and Evolution 17:1885–1895.

Niklas, K. J. 1997. The evolutionary biology of plants. University of Chicago Press, Chicago.

O'Hara, R. J. 1992. Telling the tree: narrative representation and the study of evolutionary history. Biology and Philosophy 7: 135–160.

Osborn, H. F. 1905. The ideas and terms of modern philosophical anatomy. Science 21:959–961.

Patterson, C. 1982. Morphological characters and homology. Pp. 21–74 *in* K. Joysey and A. Friday, eds. Problems of phylogenetic reconstruction. Academic Press, London.

Phillips, T. L., and W. A. DiMichele. 1992. Comparative ecology and life-history biology of arborescent lycopsids in Late Carboniferous swamps of Euramerica. Annals of the Missouri Botanical Garden 79:560–588.

Pryer, K. M., H. Schneider, and S. Magallón. 2004. The radiation of vascular plants. Pp. 138–153 *in* Cracraft and Donoghue, 2004.

Remy, W., P. G. Gensel, and H. Hass. 1993. The gametophyte generation of some early Devonian land plants. International Journal of Plant Sciences 154:35–58.

Renzaglia, K. S., R. J. Duff, D. L. Nickrent, and D. J. Garbary. 2000. Vegetative and reproductive innovations of early land plants: implications for a unified phylogeny. Philosophical Transactions of the Royal Society of London B 355:768–793.

Rudall, P. J. 1991. Lateral meristems and stem thickening growth in monocotyledons. Botanical Review 57:150–161.

Sanderson, M. J. 1998. Reappraising adaptive radiation. American Journal of Botany 85:1650–1655.

Sanderson, M. J., and M. J. Donoghue. 1989. Patterns of variation in levels of homoplasy. Evolution 43:1781–1795.

———. 1996. The relationship between homoplasy and confidence in a phylogenetic tree. Pp. 67–89 *in* M. Sanderson and L. Hufford, eds. Homoplasy and the evolutionary process. Academic Press, San Diego.

Sattler, R. 1984. Homology—a continuing challenge. Systematic Botany 9:382–394.

———. 1991. Process homology: structural dynamics in development and evolution. Canadian Journal of Botany 70:708–714.

Schneider, H., K. M. Pryer, R. Cranfill, A. R. Smith, and P. G. Wolf. 2002. Evolution of vascular plant body plans: a phylogenetic perspective. Pp. 330–363 *in* Q. Cronk, R. Bateman, and J. Hawkins, eds. Developmental genetics and plant evolution. Taylor and Francis, London.

Soltis, P. S., D. E. Soltis, M. W. Chase, P. K. Endress, and P. R. Crane. 2004. The diversification of flowering plants. Pp. 154–167 *in* Cracraft and Donoghue, 2004.

Stewart, W. N., and G. W. Rothwell. 1993. Paleobotany and the evolution of plants, 2d ed. Cambridge University Press, New York.

Tomlinson, P. B. 1995. Non-homology of vascular organization in monocotyledons and dicotyledons. Pp. 589–622 *in* P. Rudall, P. Cribb, D. Cutler, and C. Humphries, eds. Monocotyledons: systematics and evolution, Vol. II. Royal Botanic Gardens, Kew, U.K.

Tomlinson, P. B., and M. H. Zimmermann. 1969. Vascular anatomy of monocotyledons with secondary growth—an introduction. Journal of the Arnold Arboretum 50:159–179.

Vamosi, J. C., S. P. Otto, and S. C. H. Barrett. 2003. Phylogenetic analysis of the ecological correlates of dioecy in angiosperms. Journal of Evolutionary Biology 16:1006–1018.

Zanis, M. J., D. E. Soltis, P. S. Solits, S. Mathews, and M. J. Donoghue. 2002. The root of the angiosperms revisited. Proceedings of the National Academy of Sciences USA 99:6848–6853.

Zimmermann, W. 1965. Die Telomtheorie. Fischer, Stuttgart.